




## Research Article

# No evidence for pronounced mate-finding Allee effects in the emerald ash borer (*Agrilus planipennis* Fairmaire)

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## Abstract

Allee effects are density-dependent barriers that can impact species establishment and population growth, such as through reduced mating success at low population densities. The emerald ash borer, *Agrilus planipennis* Fairmaire, has been extremely successful at rapidly expanding its North American range. The impact of mate-finding Allee effects (an important type of component Allee effect) early in the invasion period of the emerald ash borer remains unknown. We measured mating success in females as a function of beetle abundance in Halifax, Canada, where the emerald ash borer was recently discovered, and in Connecticut USA, where it has been established for over a decade. We measured relative population abundance and sampled beetles using different strategies. In Halifax, we placed clusters of prism traps along an invasion gradient of emerald ash borer abundance, and in Connecticut, we collected beetles from foraging *Cerceris fumipennis* females. We dissected female reproductive tracts to measure mating success. We fit a linear regression to the mating success of females as a function of beetle abundance. We found that emerald ash borer did not present a pronounced mate-finding Allee effect as there was no positive relationship between female mating success and abundance. Lack of pronounced component Allee effects that impede population growth may explain rapid range expansion in species that are highly invasive, such as the emerald ash borer.

**Key words:** Allee effects, emerald ash borer, invasion biology, invasion dynamics, mating success, population ecology



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## Introduction

Introduced species must overcome several ecological barriers before establishment and population growth can occur. Such barriers include Allee effects, density-dependent mechanisms that prevent low-density populations from increasing (Allee 1938; Taylor and Hastings 2005; Liebhold and Tobin 2006; Gertzen et al. 2011). Allee effects often occur in introduced species because populations are small, leading to difficulty finding mates, inbreeding depression, high predation, or difficulty acquiring food (Courchamp et al. 1999, 2008; Kramer et al. 2009).

An introduced species that has caused widespread ecological and economic damage throughout North America in a relatively short period is the emerald ash borer (hereafter referred to as EAB), *Agrilus plannipennis* Fairmaire (Coleoptera, Buprestidae). It has been introduced from eastern Asia to North America and

eastern Europe (Cappaert et al. 2005; Valenta et al. 2017). In North America, it was first discovered in Detroit, MI, in 2002 (Haack et al. 2002), and has since spread rapidly throughout the eastern USA and Canada.

The rapid expansion of EAB in its North American range can be attributed to the movement of ash materials such as saplings, wood chips, and untreated firewood (Cappaert et al. 2005). Human transport of these products has led to the introduction of many satellite EAB populations across both planted and natural ash ranges in North America (Muirhead et al. 2006). EAB has infested more than 1,400 counties in Canada and the United States (Emerald Ash Borer Network 2022; United States Department of Agriculture 2023) and has caused substantial mortality to ash trees in North America (Herms and McCullough 2013).

Population modelling has shown that EAB could be managed if invading populations were under a strong demographic Allee effect (McDermott and Finnoff 2016) – that is, if there were a threshold population density below which low mating success leads to a negative population growth rate (Fauvergue 2013). Each long-distance movement would subject the insect to the ecological pressures of establishing new populations at low population densities. However, incipient EAB populations are difficult to monitor accurately, affecting the ability to manage populations early in the infestation (Siegert et al. 2014; Ryall 2015). Consequently, the importance of Allee effects during the establishment period of EAB is largely unknown. Specifically, empirical studies on density-dependent mate-finding in EAB remain limited (McDermott and Finnoff 2016). Mating failure has been suggested as a mechanism (a “component Allee effect”) for negative population growth rates at low population densities due to the inability of males and females to locate each other when sparsely distributed on the landscape (Fauvergue 2013). Pronounced mate-finding Allee effects are known for at least some invasive forest pests, including brown spruce long-horn beetle *Tetropium fuscum* Fabricius (Coleoptera, Cerambycidae) (Rhainds et al. 2015) and the spongy moth *Lymantria dispar dispar* Linnaeus (Lepidoptera: Lymantridae) (Sharov et al. 1995; Contarini et al. 2009). Whether a similar effect exists for EAB is thus an evident and important question.

We examined the mating success of EAB as a function of beetle abundance in two distinct geographical locations. First, we studied a recently established satellite population in Atlantic Canada. In 2018, EAB were detected in a city park in the northeastern edge of the Halifax Regional Municipality of Nova Scotia. We measured female EAB mating success as a function of male abundance in scattered ash tree clusters along the current EAB range in Halifax, collecting beetles in pheromone-baited traps. Second, we studied a population in Connecticut, USA, about 800 km SW of Halifax. In this case, we measured female EAB mating success in individuals collected as prey by a native wasp and used the proportion of EAB captured by wasps among all beetle prey as a proxy measurement of abundance (Rutledge 2023; Rutledge and Clark 2023). In each population, we hypothesized that if pronounced mate-failure Allee effects were present, there would be a positive relationship between female mating success and beetle abundance. In contrast, if female mating rates were similar across all populations with different abundances, it would suggest that female mating failure at low population densities may not be an important factor in EAB population establishment (Fauvergue 2013). We did not find evidence for a pronounced mate-finding Allee effect in EAB in either location. However, we cannot rule out mate-finding Allee effect occurring below the beetle abundances we observed, nor Allee effects due to other density-dependent factors such as predation.

## Methods

### Study system

EAB can be distinguished from native North American wood borers (Coleoptera, Buprestidae) by its metallic green coloration and metallic red on the dorsal portion of the abdomen (Wei et al. 2004; Volkovitsh et al. 2019). Adults lay eggs in bark crevices of ash trees in the summer. Larvae emerge and feed on the phloem tissue beneath the bark, causing significant damage to the conductive tissues of the tree (Cappaert et al. 2005). EAB overwinter as late larvae or pupae and emerge from the bark the following summer (Bauer et al. 2004; Poland et al. 2011) although under conditions of high tree vigour or limited growing degree days, it can take individuals two years to complete their lifecycle (Wang et al. 2010). Peak adult emergence occurs at 450–500 °C (DD<sub>10C</sub>) (above 10 degrees) and sharply ends at 833 (DD<sub>10C</sub>) (Bauer et al. 2004; Tobin et al. 2021). Adult EAB will typically live for three to six weeks, when they feed on ash foliage, search for mates, and oviposit on ash trees, *Fraxinus* spp. (Bauer et al. 2004; Cappaert et al. 2005). Both male and female beetles can mate with several partners (Rutledge and Keena 2012). Sperm is transferred as a spermatophore to the female, and when the spermatophore dissolves, the sperm, bundled in groups of approximately 50 sperm in hyaline sheaths, are transported into the spermatheca bulb (Rutledge and Keena 2019) and can be observed by dissection and microscopic examination. The presence or absence of sperm in the spermatheca indicates the mating status of a given female.

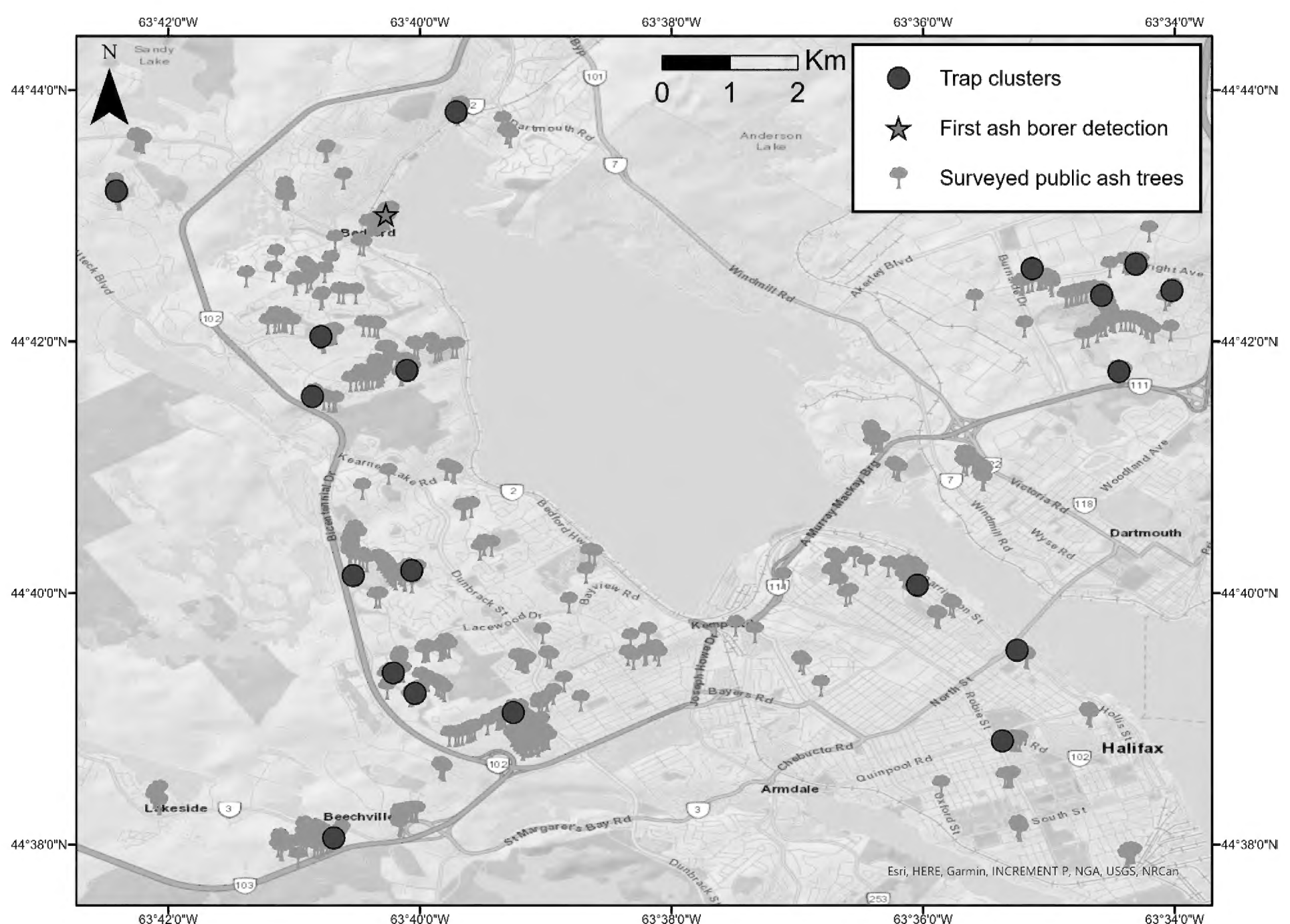
### Site and sampling design: Nova Scotia

We conducted the Nova Scotia study in 2022 using urban street trees and parks in the Halifax regional municipality (44°40'N, 63°36'W). The Bedford Basin, a large, enclosed bay, bisects the Halifax regional municipality. EAB was first detected at Harry DeWolf Park in 2018, at the interior tip of this basin. Halifax is a mid-sized city with a population of approximately 440,000 people and an area of 5,500 km<sup>2</sup>. Halifax manages approximately 49,000 public trees (City of Halifax 2020). The most common species in the Halifax urban forest are Norway maple (*Acer platanoides* Linnaeus), American elm (*Ulmus americana* Linnaeus), and red maple (*A. rubrum* Linnaeus), accounting for about 32% of all publicly surveyed trees (City of Halifax 2020). Ash trees (*Fraxinus* spp.) account for approximately 1,225 trees, or 2.5% of all publicly surveyed trees in Halifax (City of Halifax 2020). Green ash (*F. pennsylvanica* Marshall) is the most common ash species surveyed, accounting for approximately 65% of all ash trees in Halifax. Nova Scotia is within the Acadian Forest, dominated by red spruce, balsam fir, yellow birch, sugar maple, eastern hemlock, eastern white pine, and red oak (Neily et al. 2017). Ash trees sparsely populate forested regions outside of Halifax, with highest populations (18%) in the southwestern portion of the province (Beaudoin et al. 2014). While EAB may have a preference for green ash, the preference does not appear to be strong (Anulewicz et al. 2008; Pureswaran and Poland 2009). Since its discovery in Nova Scotia, the provincial government has monitored EAB populations using green prism traps. Street trees were not treated with insecticides, enabling EAB to infest trees unhindered. In 2021, parasitoid wasp releases began but their range was limited to a few hundred meters from the release site, outside of our sampling locations (Cory Hughes, Natural Resources Canada, Pers. Comm., 2022).



To measure EAB populations, we arranged green (Andermatt Canada Inc., Fredericton, New Brunswick) and purple (WestGreen Global Technologies Inc., Langley, British Columbia) prism traps in clusters of at least four ash trees (Fig. 1). Each cluster had traps on four trees, with one green and one purple trap per tree. Green traps were baited with EAB pheromones (Silk et al. 2011) (3Z-lactone, 3 mg load rate, 50 µg/day release rate, Andermatt Canada Inc., Fredericton, New Brunswick) and host kairomones (3Z-hexenol, 5 mL load rate, 50 mg/day release rate, Andermatt Canada Inc., Fredericton, New Brunswick) to increase trap catch. The attraction radius of traps baited with these pheromones is effective at approximately 28 metres from the pheromone source and as distance increases to 70 metres, becomes less effective (Wittman et al. 2021).

We chose cluster locations based on the availability ash trees on public land and at increasing distances from the initial infestation point, which in other studies has been shown to correlate with decreasing populations sizes (Mercader et al. 2009). Clusters were at least 350 meters apart to minimize trap interference (Wittman et al. 2021). Trees within clusters were at most 150 meters apart. We placed a green prism trap near the upper crown and a purple prism trap near the mid crown. Purple prism traps are reported to attract females as they resemble oviposition sites on tree bark (Francese et al. 2010). To increase trap catch, we placed traps on the south sides of the trees (Lyons et al. 2009) and placed two dead female EAB



**Figure 1.** Emerald ash borer collection in the Halifax Regional Municipality, Nova Scotia. Green circles represent sampled clusters of ash trees. Red star represents the location of the first ash borer detection in the Halifax Regional Municipality. Grey tree icons represent ash trees identified during street tree surveys.

as decoys in the upper left corner and near the center of each side of our traps (Domingue et al. 2015). We marked each decoy in white on the abdomen and head so that we didn't collect it, and we replaced as needed during weekly checks.

We measured degree days above 10 °C ( $DD_{10}$ ) from a weather station monitored by the Government of Canada in Halifax to know when to deploy and finish trap collection. We deployed traps at the beginning of EAB flight on June 3<sup>rd</sup>, 2022, at approximately 260 ( $DD_{10C}$ ), and collected them on August 15<sup>th</sup>, at approximately 745 ( $DD_{10C}$ ), when flight neared its end. We checked traps weekly, collected all the buprestid beetles into a cooler, then transferred them to a -18 °C freezer until dissection.

### Site and sampling design: Connecticut

We conducted the Connecticut study in 2013–2016 and 2022–2023, using 48 sites across the state ranging from 41.43 to 41.88°N, and from -71.88–73.50°W. Emerald ash borer was first detected in New Haven County, Connecticut, USA in 2012 (Rutledge et al. 2013). Prior to, and for the first 2 years after, the invasion purple prism traps were widely distributed throughout the state and were responsible for detections in several counties. Simultaneously, a novel survey technique known as biosurveillance (Careless et al. 2014), was implemented, and after initial county detections had been made in over half of Connecticut's eight counties this has since become the sole continuing survey. Since then, EAB has spread to all corners of the state, and has been broadly destructive (Rutledge and Clark 2023).

Biosurveillance exploits the buprestid-hunting habit of a native wasp, *Cerceris fumipennis* (Hymenoptera, Crabronidae). These solitary ground-nesting wasps use paralyzed, adult buprestid beetles to provision their brood cells. Wasps live in aggregations in sandy areas, from which they set out to hunt in the canopy of the surrounding forest. They will target a wide range of genera within the Buprestidae, limited only by prey weight and size relative to the individual female wasp, phenology, and arboreal habit. More than 100 species of beetles have been recorded as prey of *C. fumipennis* (Rutledge et al. 2013; Careless et al. 2014). The proportion of individual species in the catch depends roughly on the proportion of those species in the surrounding 1.5 km of forest canopy (Rutledge 2023). This relationship is vividly illustrated during periods of unusual abundance of particular prey items, such as during the invasion of emerald ash borer (Rutledge and Clark 2023), the increased proportion of the hemlock borer (*Phaenops fulvoguttata*) a native-secondary pest of hemlock, suffering an outbreak of hemlock wooly adelgid in the mountains of western North Carolina (Swink et al. 2013), or the correlation between the proportion of conifers surrounding a colony, and the proportion of conifer feeding beetles captured by the wasps (Rutledge 2023). Thus, relative population densities of emerald ash borer can be a good measure for estimating the ratio of EAB to other buprestids captured by the wasps at the same time and place (Rutledge and Clark 2023).

We (CER and colleagues) have been conducting biosurveillance across the state since 2010, and all beetles collected have been identified by site and date. Since 2016, all EAB have been frozen and stored after capture, and thus were available for dissection. We selected female EAB for dissection from site/year combinations for which at least 30 beetles had been collected. This ensures that the estimate of relative abundance of EAB at that site was robust.

## Identification and dissection of female EAB

For beetles captured in the prism traps, we cleaned glue residue from collected beetles using limonene. We identified and kept only EAB beetles. We identified females either based on their enlarged 1<sup>st</sup> abdominal segment and a lack of dense setae on the prosternum (Wang et al. 2010), or, for beetles not evidently expressing these characteristics, by the presence of an ovipositor on the last abdominal section. For beetles collected by biosurveillance, we chose well-preserved frozen specimens.

We dissected female reproductive systems by pulling the ovipositor with forceps, removing the reproductive tract, and mounting it onto a microscope slide. We cut the bulb of the spermatheca and gently squeezed it to push out any sperm. We stained the slide with Giemsa stain (Giemsa 1904) (Thermo Fisher Scientific, Waltham, Massachusetts, USA) to make sperm more visible. We assessed slides for sperm and scored beetles for the presence or absence of sperm. A female was considered successfully mated if we identified sperm in the reproductive tract (Rhainds 2010).

## Statistical analysis

Estimating absolute abundance for EAB in an urban area with non-random ash tree distribution is difficult, and the appropriate sampling unit (such as area or number of ash trees) is not obvious. We chose instead to work with relative estimates of abundance: total male trap catch (per tree cluster) for Halifax and proportion of EAB collected from *Cerceris* wasps (per site) for Connecticut. For the remainder of the text, we use “abundance” to refer to this relative abundance estimate of beetles. Because we are using relative estimates, we cannot directly relate our Halifax and Connecticut abundance estimates. However, this does not matter, as we are only asking whether we can detect mating-abundance relationships within each region.

To test the hypothesis that mating success increases with beetle abundance, we fit weighted linear regressions of proportion mated females as a function of male abundance, separately for EAB collected from Halifax (by tree cluster) and Connecticut (by site). We weighted each data point by one divided by the square of the difference between the upper confidence interval (CI) and the lower confidence interval (CI) to account for the greater information contained in estimates from sites with more beetles. However, unweighted regressions supported identical conclusions (results not shown). An alternative analysis for Halifax with log transformation of male abundance yielded essentially identical results (not shown).

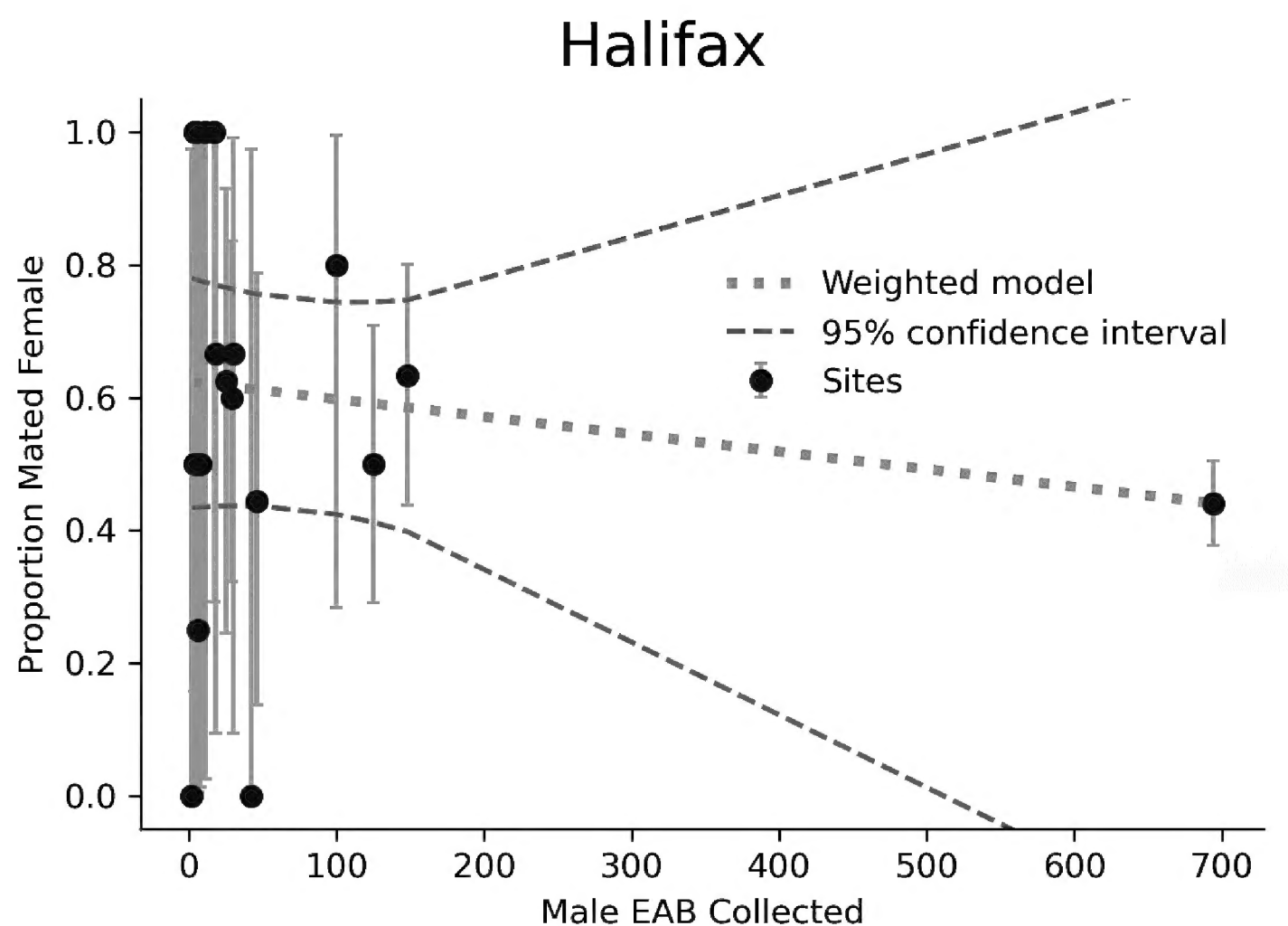
We used the Scipy (V.1.9.3) and Scikit Learn (V.1.0.2) packages in Python (V.3.9.16) to conduct all statistical analyses. We performed data visualization using the Matplotlib (V.3.6.2) and Seaborn (V.0.12.2) packages.

## Results

### Nova Scotia

We collected 1673 adult EAB (1329 males and 356 females) over the course of the study. Of the 356 females, 174 had sperm present in their spermatheca leading to a mean female mating success rate of 0.59 ( $\pm 0.072$  SE). More than half

(983 individuals) of the beetles were collected from a site nearest the invasion epicentre. The number of males significantly predicted the number of females collected within clusters ( $r^2=0.98$ ,  $p=2.5e^{-14}$ ). For every female EAB collected in traps approximately 3.7 males were collected. Male abundance was not a good predictor of female mating success ( $r^2=0.015$ ,  $p=0.63$ , 95% CI slope =  $[-1.2e-03, 7.7e-04]$ , Fig. 2). Because the confidence interval includes some weakly positive slopes, we cannot rule out a subtle mate-finding Allee effect, although we can rule out a strong one (that is, more positive slopes fall outside the 95% confidence interval).



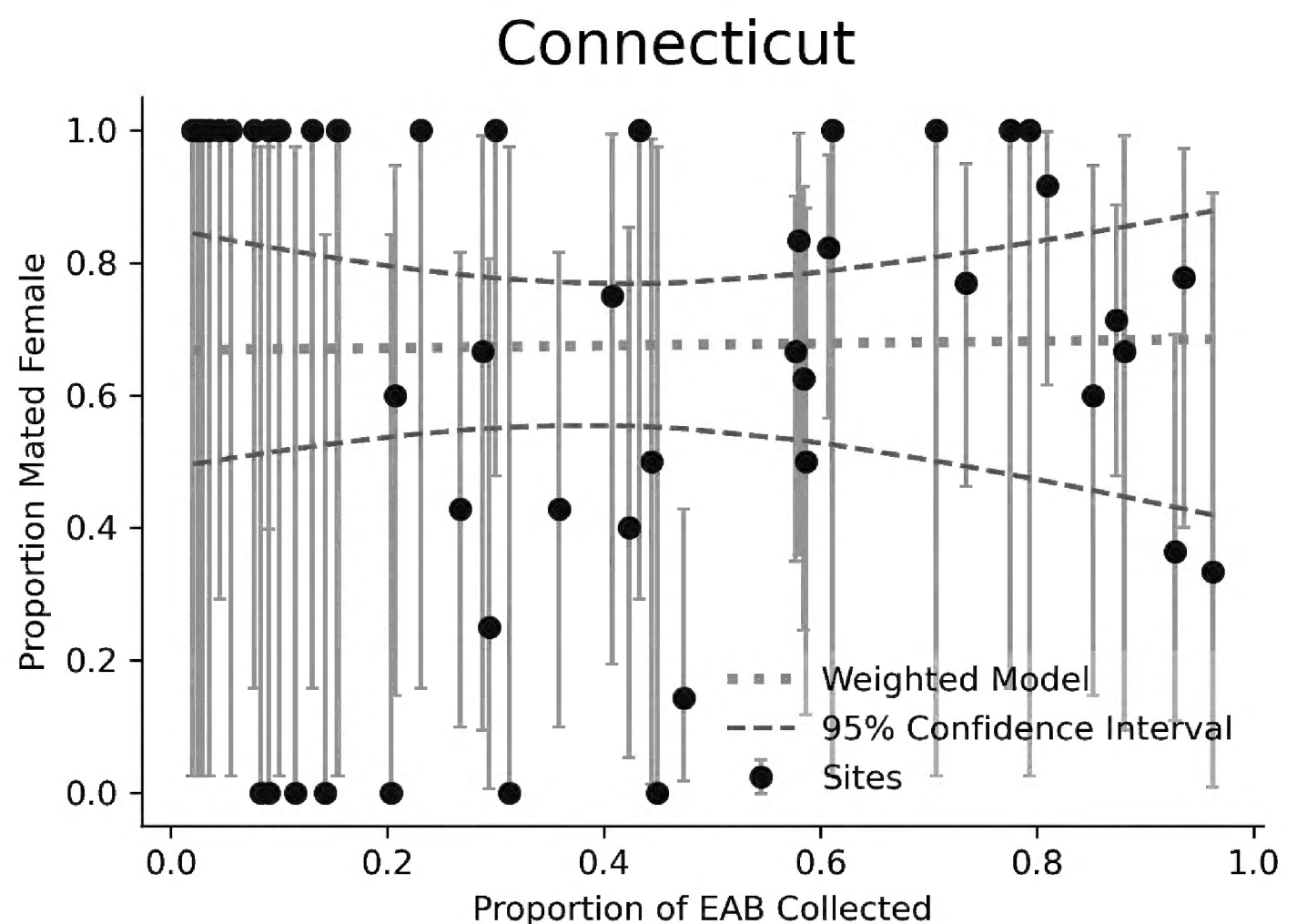
**Figure 2.** Female mating success as a function of relative male abundance. Collected from prism traps in Halifax, Nova Scotia, Canada, in 2022. Dots represent clusters of trees where beetles were trapped. Error bars represent 95% confidence intervals of the proportion of mated females at each location. The dotted red line represents the slope of the weighted linear regression (not significant). The dashed blue line represent 95% confidence intervals of the linear regression.

## Connecticut

Relative abundance of EAB, as measured by proportion of EAB to other beetles collected, ranged from 0.020–0.935 with a median abundance total of 0.388 from 48 sites. The number of beetles collected at sites from which dissected beetles were chosen ranged from 31–288 with a median sample size of 63. We dissected 249 female EAB. Of the female EAB dissected, 168 had sperm present in their spermatheca indicating successful mating while 81 did not successfully mate as indicated by the lack of sperm.

Population abundance did not significantly predict female mating success ( $r^2=0.000$ ,  $p=0.9$ , 95% CI slope =  $[-0.38, 0.34]$ , Fig. 3). Because the confidence interval includes some weakly positive slopes, we cannot rule out a weak mate-finding Allee effect, although we can rule out a pronounced one (that is, more positive slopes fall outside the 95% confidence interval).





**Figure 3.** Female mating success as a function of relative EAB abundance. Collected from *Cerceris fumipennis* wasps in Connecticut, United States, from 2014–2016 and 2022–2023. Dots represent geographically distinct communities within Connecticut. Error bars represent 95% confidence intervals of the proportion of mated females at each location. The dotted red line represents the slope of the weighted linear regression (not significant). The dashed blue line represents 95% confidence intervals of the linear regression.

## Discussion

Allee effects can have important influences on establishment success of non-native species, even determining whether populations continue to grow in the invaded habitat. Allee effects have been shown to influence population dynamics and suppress populations between outbreaks in both non-native forest insects such as the spongy moth (*Lymantria dispar dispar* Linnaeus) (Liebhold and Bascompte 2003) and native species such as spruce budworm (*Choristoneura fumiferana* Clemens) (Régnière et al. 2013) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Raffa and Berryman 1983).

Mate-finding Allee effects have been demonstrated in very few forest insect systems because it is typically difficult both to observe individuals at low densities and to determine mating status of those individuals (e.g., Kramer et al. 2009; Rhainds 2010). However, we were able to test for mate-finding Allee effects in two different regions, using two different approaches for estimating EAB abundance. In neither case did we find evidence for pronounced mate-finding (component) Allee effects. The proportion of female beetles that were successfully mated was consistent, despite varying male densities, suggesting that mate-finding failure may not occur in incipient populations of EAB. If an Allee threshold exists, the threshold occurs at even lower population densities than those we measured. Prism traps and biosurveillance have similar detection thresholds, and are generally used as early detection strategies for new infestations (Francese et al. 2013; Rutledge et al. 2013; McCullough and Poland 2017) because they can be effective at beetle densities far too low for direct census (by branch dissections). It is certainly possible that



mate-finding Allee effects kick in at densities too low even for these techniques to measure. Since this also means densities too low for infestations to be detected and studied, it would be a major challenge to document such extremely low-density Allee effects if they exist. Experimental manipulation of population densities could yield more power and better precision in estimating the mating-density relationship but would be both logistically and ethically challenging.

Studying low-density populations, ones that are frequently affected by component Allee effects, remains challenging due to the difficulty of finding small enough populations but detecting enough individuals to derive meaningful statistical conclusions (Liebhold and Bascombe 2003; Kramer et al. 2009). Once individuals are detected in high enough populations, they may no longer be affected by component Allee effects (McDonald 2004). Therefore, studying low-density populations can require significant amounts of resources to receive meaningful empirical measurements. We designed our study to be comprehensive in its ability to collect sufficient individuals by increasing sampling efforts in the Halifax study and collecting over a long time period in the Connecticut study.

Our results suggest that EAB is not subject to pronounced mate-finding (component) Allee effects through the range of abundances we studied. We found approximately half of collected EAB females were mated even at our lowest populations. This contrasts with some studies of other introduced species such as the brown spruce longhorn beetle (Rhainds et al. 2015) and spongy moth (Sharov et al. 1995; Johnson et al. 2006), in which mating success declines close to zero at low population density. In the case of the brown spruce longhorn beetle, invasion appears to have stalled at the current range edge, possibly due to mating failure (Rhainds et al. 2015; Anderson et al. 2022).

Even at our highest-abundance sites, a substantial fraction of females often remained unmated: mated fractions reached only 60–70% in Halifax, and 40–80% in Connecticut. For brown spruce longhorn beetle, Rhainds et al. (2015) found mating rates at around 80% in the largest populations, while for spongy moth, Sharov et al. (1995) found mating rates up to 100%. However, we used two sampling techniques that are designed to be very efficient at low beetle densities, and it's possible that sampling simply took females out of circulation early in their lives.

Mate-finding Allee effects in low-density populations generally exist when organisms are sparsely distributed in space and encounters among individuals are low. However, mate-finding difficulties can potentially be overcome if mate-finding is particularly efficient. This might be especially true in systems where mate-finding is multimodal, as it is for EAB. EAB uses multiple cues to identify host trees and find mates. Both males and females are attracted to volatiles of stressed ash trees, particularly 3Z-hexenol, a component of ash foliage (De Groot et al. 2008). In addition, they are visually attracted to wavelengths in the green range (530–540 nm) (Crook et al. 2009; Francese et al. 2010) as they spend a two-week maturation period feeding on foliage before mating. Females, at least, are also attracted to purple traps, the colour resembling that of tree bark onto which they oviposit (Lelito et al. 2007; Rodriguez-Saona et al. 2007; Crook et al. 2009; Francese et al. 2010). Finally, females produce a pheromone, (3Z)-lactone, which is attractive to males (Silk et al. 2011; Ryall et al. 2013; Silk and Ryall 2015). We took advantage of these behaviors in our Halifax study by deploying purple and green pheromone-baited traps; this is a common approach in studies of forest pest insects (e.g., Régnière et al. 2013; Parker et al. 2020). Nevertheless, we were surprised by

the ability of EAB to locate mates even in the very low-abundance populations we studied. While EAB are not known to use their pheromones for long-range attraction, we speculate that the multimodal nature of host and mate-finding behaviours in EAB, including attraction to host volatiles, allows them to aggregate on trees and potentially overcome mate-finding Allee effects, at least at the densities measured in our study. In turn, this ability to find mates even at rather low population densities may help explain the rapid spread of EAB (Ward et al. 2020) across its invasive North American range.

Understanding the strength of Allee effects on invasive species remains important, as it can impact how management strategies are best implemented. Invasive species experiencing Allee effects may be better managed at low densities (Tobin et al. 2011), and may have a longer window for detection before new populations are unmanageable. For species like EAB, the lack of a pronounced component Allee effect may explain the difficulties encountered in population management following detection. Eradication may be possible only at extremely early stages of local establishment, and management resources may be better spent reducing human-assisted spread.

## Conclusion

Risk modelling of long-distance dispersal of EAB has shown that Allee effects are likely to be an important determinant of its spread (Caouette 2023). However, we have found that EAB does not show a pronounced mate-finding Allee effect even at the lower population densities we were able to study. It is, of course, possible that other component Allee effects are present; further work would be necessary to test such hypotheses. However, the lack of mate-finding Allee effects, in combination with other factors such as the widespread planting of clonal ash cultivars and lack of natural enemies, may contribute to the rapid spread of EAB in North America and elsewhere. Allee effects remain an important and seldom-studied aspect of biological invasions. By studying population dynamics in consideration of Allee effects, we can better understand population growth and invasiveness of non-native species to determine the best methods to manage invasive species.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: Alexandre P. Caouette, Claire E. Rutledge, Stephen B. Heard, Deepa S. Purewaran. Data Curation: Alexandre P. Caouette. Formal Analysis: Alexandre P. Caouette. Funding

Acquisition: Stephen B. Heard, Deepa S. Pureswaran, Claire E. Rutledge. Investigation: Alexandre P. Caouette, Claire E. Rutledge. Methodology: Alexandre P. Caouette, Claire E. Rutledge. Project Administration: Alexandre P. Caouette, Claire E. Rutledge. Resources: Stephen B. Heard, Deepa S. Pureswaran. Software: Alexandre P. Caouette. Supervision: Stephen B. Heard, Deepa S. Pureswaran. Validation: Alexandre P. Caouette. Visualization: Alexandre P. Caouette. Writing – Original Draft Preparation: Alexandre P. Caouette. Writing – Review & Editing: Alexandre P. Caouette, Stephen B. Heard, Deepa S. Pureswaran, Claire E. Rutledge

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## Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information. We have submitted data to DRYAD at the following URL: <https://doi.org/10.5061/dryad.000000097>.

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## Supplementary material 1

### Number of beetles caught in a cluster based on the distance from the invasion epicentre

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Data type: docx

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